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THE POTENTIAL ROLE OF THE STERILITY METHOD FOR INSECT POPULATION CONTROL WITH SPECIAL REFERENCE TO COMBINING THIS METHOD WITH CONVENTIONAL METHODS

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THE POTENTIAL ROLE OF THE STERILITY METHOD FOR INSECT POPULATION CONTROL WITH SPECIAL REFERENCE TO COMBINING THIS METHOD WITH CONVENTIONAL METHODS

By E. F. Knipling [1/]
Entomology Research Division, Agricultural Research Service

The release of sterile insects offers a useful new method for controlling or eliminating populations of certain insects. The merits and limitations of the method for use against the wide range of insects that we must contend with cannot be fully determined on the basis of current knowledge. However, with the information and experience already gained and further study of the basic principles involved, there is every reason to believe that the technique, used alone or integrated with other methods, can have broad application for the control or eradication of a number of our most destructive insects. The need is acute for more desirable, as well as more economical, ways to regulate populations of certain key insect species that cause high economic losses, and which, in addition, necessitate costly and continuing control efforts. Current control measures for some of these major pests contribute substantially to the accumulation of insecticides in our total environment. Moreover, to control key insect species, it is necessary to employ broad spectrum insecticides, which have adverse effects on natural enemies, necessitating a more intensive effort to control other pests.

The sterile-insect technique will not be practical for controlling or eliminating established populations of most of our destructive insect species. The method will not be feasible for those that have a wide host range, are sporadic in appearance, or which do not cause high economic losses. An insect pest might be of great importance on minor crops, but the total economic value of the crops may not justify the costly control or eradication programs that most likely would be involved in the mass production and release of large numbers of sterile insects. This same line of reasoning, however, may not hold for insects that have a restricted host range.

1/ The writer is indebted to many members of the Entomology Research Division staff for information on insect biology, ecology, behavior, and population dynamics, which is so vital to an overall appraisal of the potential value of the sterile-insect-release method. He is especially indebted to L. D. Christenson, Chief of the Fruit and Vegetable Insects Research Branch.

The Entomology Research Division, which has pioneered the sterile-insect-release procedure, receives numerous inquiries regarding the feasibility of the method for controlling or eliminating various kinds of insects. In many instances, because of the nature of the pest and the circumstances involved, little or no encouragement can be offered that the technique will be practical. On the other hand, there are many insect problems of great importance in this country and in other parts of the world that, on careful analysis, would appear to justify serious effort by scientists to explore the potentialities of the method. Delay in the initiation of investigations on some of these problems may be due to a general lack of appreciation of the full potential of the technique, and how it might be integrated with other methods of control.

Accordingly, this report will discuss, in more detail than in previous publications, the principles and factors that must be considered in appraising the potentialities of the sterile-insect-release method for controlling an insect population. Special effort will be made to indicate how the method could be integrated with other methods of control. This more detailed analysis will consider, primarily, the role that the method might have in the control of well-established insect populations. Conceivably, the sterile-insect-release method could be useful in eliminating incipient infestations of almost any bisexual insect species if the basic information and procedures have been developed, and if a program can be put into effect before the pest population spreads and increases to such numbers that it would not be economically feasible to produce the number of sterile insects required for eradication.

There is a tendency to regard the sterile-insect-release method as impractical for controlling or eliminating established insects when the natural population consists of hundreds of millions of individuals in relatively large areas, because of the even greater numbers of the insect that would have to be produced for sterilization and release. Such a conclusion is not justified without carefully weighing all of the factors that have a bearing on the problem. It is necessary, first of all, to have a full understanding of the sterility principle and its inherent merits and limitations. The principles and basic requirements that must be met before application of the sterility technique is practical have been discussed in other publications. The requirements, as published, are still valid. However, it seems desirable to treat various aspects of the subject in greater depth, and to offer more specific suggestions as to how the technique might be integrated with other control or eradication methods.

The sterility technique relates to the mass production and release of sterile insects. Sterilizing insects in the natural population should eventually provide great opportunities for controlling or regulating pest populations, but this approach will not be discussed in this report because ways to use currently available chemical sterilants effectively and safely have not yet been clearly demonstrated.

PRINCIPLES INVOLVED

Normal Trends of Insect Populations

The way that sterile-insect releases affect population trends can be demonstrated by the use of hypothetical, but reasonably realistic, models.

Unless the principles are well understood and appropriately applied in relation to the population trend that is characteristic for the particular insect to be controlled, in its different ecological situations, failure is likely to result in attempts to use sterile insects for practical control. The model that follows is representative of the usual trend of many of our well-established insect populations.

Model 1.—Theoretical trend of a hypothetical uncontrolled insect population increasing at a five-fold rate per generation

Generation	Number of insects per unit area
Parent	1,000,000
F_1	5,000,000
F_2	25,000,000
F_3	125,000,000

The above is reasonably realistic for many insect populations that are increasing from a low level in the population cycle. There is a point, however, in the population cycle of any pest, after which no further increase can be expected, because all organisms eventually reach a maximum density that the environment can maintain. The rate of increase for each pest can be expected to vary, depending on many factors, and for most species we cannot identify and properly weigh all of the factors involved. We know very well, however, that the biotic potential of most insects exceeds by far the actual rate of increase from one generation to the next. An insect population already well adjusted to its environment seldom comes even close to achieving its maximum potential increase rate because of the many environmental hazards. Newly established pests are likely to achieve a much higher rate of increase until some degree of natural balance with the environment is attained. It is difficult to determine the normal or representative rate of increase of different insects, even in a well-balanced environment. Such knowledge is of basic importance, regardless of the method of control, but relatively little precise information is available on the subject.

In the absence of definitive data, even a rough estimate of the normal rate of increase is so vital to an appraisal of the potentialities of the sterile-insect-release method, the writer has attempted by devious ways to gain as much information as possible on the question as it relates to specific insects. As a working hypothesis, it has been concluded that a five-fold rate per generation is a reasonably valid rate of increase for most well-established insect pests. It is obvious that the rate of increase will vary, depending on the species and on the conditions under which the insect is existing. Some insects have an inherently low increase rate. The tsetse fly is a good example. The increase rate for these insects probably seldom exceeds two-fold per generation. A ten- or even twenty-fold increase may occur for other insect species under favorable conditions.

In considering ways to regulate a given insect population, rate of increase is one of the most vital factors to keep in mind.

Trends of an Insect Population Subjected to Usual Methods of Control

If we know the normal trends of an insect population, we can then make a good estimate of the effects on such trends of different methods of control. Since the sterile-insect-release method, as well as other methods of control affect population trends in different ways, we should consider this point carefully.

Model 2.—Trend of an insect population subjected to control by insecticides or similar means, when the level of kill is 90 percent each generation. An increase rate of five-fold is assumed for the insects surviving the treatment

Generation	Number of insects per unit area (Population actually treated)
Parent	1,000,000
F_1	500,000
F_2	250,000
F_3	125,000
F_4	62,500

If 90 percent of an existing population is destroyed, and the surviving 10 percent increases at a five-fold rate, the net effect will be to reduce the population by half. This is the pattern established for the model.

The degree of control obtained for various insect populations under treatment with insecticides or similar methods obviously varies, depending on the insect, the control measure employed, the schedule of treatments, and the manner in which the treatments are applied, as well as other factors. For some insects, the available materials and methods may be more effective than 90 percent, and for others, less effective. In some cases, currently available control measures properly applied may be capable of completely eliminating the portions of the insect population actually exposed to the treatment.

Failure to achieve complete elimination of a pest population may be the result of neglect by some growers, the presence of abandoned hosts, presence of wild hosts, lack of coordination in control efforts, presence of some of the population in hibernation, and other reasons. It should be mentioned that the model assumes 90-percent control per generation. For insects that are developing and emerging over a period of time, which is usual for most insects, it may take several applications during a generation to achieve the 90-percent level of control for that generation.

Even though for many insects the level of control, or rate of increase, may differ substantially, for the purposes of this report the model will serve to explain the principles involved in controlling insect populations by the use of insecticides. Any reasonably high level of control, if sustained over a period of several generations, has a drastic effect on an insect population, in relation to an uncontrolled population. Note comparative trends in models 1 and 2. At the same time, it is difficult to reach the zero level in an insect population by following conventional methods of control if the initial population is fairly high. If the calculation in model 2 were continued for subsequent generations, we would find that a zero population level would not be reached until treatments had continued for 18 generations. If the level of control were 99 percent for each generation, it would take treatments for five generations to achieve theoretical zero. The most significant point to note in the model is that the rate of decline in the population, theoretically, will remain constant for each generation regardless of the number of insects present. In actual practice, however, the rate of decline might become less and less each generation. Certain factors regulating the survival rate of the organisms may cease to function after the application of insecticides begins.

Parasites and predators generally play a vital role in keeping the normal rate of increase down to a reasonable level. If most of the parasites and predators are destroyed, we might then expect a ten-fold increase per generation for those insects that are not killed by the insecticides. In such event, after a few treatments with insecticides, the population would show no further decline. For the purpose of this report, however, we will assume that each insecticide treatment requires the same dosage rate but has a constant effect on the total population, and in such case the rate of decline in the population remains constant.

Another point of great importance to note in model 2 is that the insecticide treatments are highly efficient in terms of numbers of insects killed when the natural population is high, but they are inefficient when the population is low. In the first

generation the treatment kills 900,000 individuals. In the F_4 generation the kill is about 56,000 individuals. In subsequent generations, each treatment, theoretically, still kills 90 percent of the population, but the actual number of insects killed becomes lower and lower. Near the point of extinction for the population, treatments may be required over an extensive area to kill only a few insects. This is typical of pest eradication programs involving the use of insecticides, as observed in actual practice.

It should be pointed out that to reverse the trend of an insect population that is increasing at a five-fold rate per generation, it would be necessary to destroy or remove more than 80 percent of the individuals in the total population each generation, assuming that all other hazards remain constant. If the level of kill falls below 80 percent each generation, the population will increase in spite of control efforts.

Trends of an Insect Population Subjected to Competition by Sexually Sterile Insects

We will now consider the theoretical effect of competing sterile insects on an insect population when the initial release rate is high enough to start a downward trend in the natural population. This is shown in model 3.

Model 3.—Trend of an insect population subjected to control by the sustained release of competitive sterile insects, when 90 percent of the total population in the first generation consists of sterile insects that have been released

Generation	Insects per unit area			
	Fertile insects	Sterile insects	Ratio of sterile to fertile insects	Insects reproducing
	Number	Number	Ratio	Number
Parent	1,000,000	9,000,000	9:1	100,000
F_1	500,000	9,000,000	18:1	26,316
F_2	131,625	9,000,000	68:1	191
F_3	9,535	9,000,000	942:1	10
F_4	50	9,000,000	180,000:1	0

It may be noted that the sterile-insect releases achieve a much more drastic effect than conventional control methods, when the initial treatment is 90 percent effective in preventing reproduction. The first release at the rate of 9,000,000 sterile insects, theoretically, has the same effect as the initial treatment of the population with an insecticide, since this would reduce the reproduction rate by 90 percent. However, the continued release of sterile insects at the initial rate will cause a progressively greater effect in reducing the reproductive rate of each subsequent generation. This is one of the most significant points to keep in mind in appraising the relative merits of the two systems of control. The sterile-insect-release method is highly inefficient when the number of insects in the population is high, but is highly efficient when the natural population is low--just the opposite of the effect of insecticide treatments. This, then, is our clue to how we can profitably integrate the two systems of control.

It should be emphasized at this point that it is essential that the rate of sterile-insect releases be high enough to start a downward trend in the natural population in order to take full advantage of this method of control. If conventional methods of destroying pest populations and the sterile-insect-release method are equally effective in the first generation, but the level of control in each case is below that required to start a downward trend, the sterile insects become progressively less efficient in each subsequent generation, whereas, the effect of the conventional method remains constant. Thus, the population subjected to sterile insects increases at a more rapid rate. This may be noted by studying theoretical model 4.

Model 4.—Comparative trends of two similar insect populations, one subjected to treatments each generation by insecticides, the other by sterile-insect releases. The degree of control is equal in the first generation for both treatments but below the level necessary to prevent an increase in population

Generation	Uncontrolled population (Increase rate, 5X)	Insecticide treatments, 75-percent kill each generation	Sterile insect releases at the rate of 3,000,000 each generation		
		Natural population	Natural population	Sterile population	Ratio of sterile to fertile insects
	Number	Number	Number	Number	
Parent	1,000,000	1,000,000	1,000,000	3,000,000	3.0 :1
F_1	5,000,000	1,250,000	1,250,000	3,000,000	2.4 :1
F_2	25,000,000	1,562,500	1,838,235	3,000,000	1.6 :1
F_3	125,000,000	1,953,125	3,475,665	3,000,000	0.87:1
F_4	125,000,000	2,441,405	9,294,115	3,000,000	0.32:1

In a pilot eradication experiment conducted on Rota in 1961-62 by the Division's Hawaii laboratory, failure to adequately overflood the natural population of the oriental fruit fly (Dacus dorsalis Hendel) resulted in failure to achieve eradication. Allowing for some loss in competitiveness of the irradiated flies released, the effective ratio of sterile to fertile insects was probably less than 5 : 1. A marked delay in seasonal buildup of flies was apparent when compared with previous records, but trapping records indicated a trend not unlike that shown in model 4 for the hypothetical population subjected to the release of sterile insects. Failure to achieve the objective in this case was not a failure of the principle of control by the use of sterile insects. The results were in line with those that could have been expected under the circumstances. Research resources were inadequate to produce the number of sterile flies required in this case. However, the failure emphasized the necessity of assuring an adequate rate of overflooding of the natural population with sterile insects. Based on this experience, additional experiments using sterile-insect releases for eliminating populations of the melon fly (Dacus cucurbitae Coquillett) and the oriental fruit fly were undertaken under conditions that assured adequate overflooding rates, and under these conditions the method proved highly successful.

Trends of an Insect Population Subjected to an Integrated Program of Sterile-Insect Releases and Conventional Methods of Control

When an insect population is too high to manage with sterile releases, even at the lowest level in the normal seasonal cycle, consideration should be given to first reducing the natural population by conventional means to a level that would make it practical to adequately inundate the natural population by the release of sterile insects. Theoretically, this approach offers the greatest potential for employing the sterile-insect-release method for practical control or eradication programs. In the first oriental fruit fly experiment on the Island of Rota already alluded to, it would have been practical without too much cost or effort to substantially reduce the natural population with protein hydrolysate bait sprays or by the use of methyl eugenol for male annihilation before initiating sterile-insect releases. In line with the earlier discussion, these methods would be highly efficient when the population is high, but progressively less efficient when it is low, so that a combination of the chemical control and sterile-insect releases would have been the most practical procedure to follow.

It is the writer's view that the potentialities of an integrated program involving the use of sterile insects, has not been given due consideration by scientists when estimating the value of sterile insects for the control of any given insect species. It may be desirable, therefore, to consider certain hypothetical models in an effort to explore the theoretical advantages of the combined approach. One procedure, although not necessarily the best one, would be to institute an intensive program of control by conventional methods so as to reduce a high population to levels that could then be managed more economically by the subsequent release of sterile insects.

In model 5, such a system of prior reduction of the original population was established by the intensive use of insecticides for several generations. In the hypothetical model, three treatments would reduce the natural population to one-eighth of the original level. At this level, it would require sterile-insect-release rates only one-eighth as high as would have been necessary for the original population. A constant release rate for four generations would then provide theoretical elimination, whereas it would have necessitated treatments with insecticides for about fifteen additional generations to achieve theoretical zero population.

The manner in which the two systems can be integrated for most effective results will depend on the biology of the insect, the control procedures normally employed, the stage of the insect that can be controlled, and other factors. By considering these factors, it should be possible to develop an integrated program that is more effective and practical than the one projected in model 5. If the insects within the same generation are subjected to the two systems of control simultaneously without interference—for example, if the insecticide were applied against the immature stages, and sterile insects were released to compete with the adult progeny that emerge—the combined effect of the two systems would be much more drastic than indicated in model 5. How to conduct the integrated program for optimum effect would depend on the insect and the control methods used. Different methods of conventional control might be employed. A nonresidual insecticide might be employed for a series of treatments to reduce the natural adult population, immediately followed by the release of sterile insects that would compete with the surviving adults and those that emerge from immature stages until the next insecticide treatment is made.

Model 5.—Relative trends of insect populations subjected to repeated insecticide treatments alone, as compared with a program of insecticide treatments for three generations followed by the release of sterile insects

Generation	Normal trend (Increase rate, 5X)	Control by insecticides at 90-percent level	Insecticide treatments, followed by sterile-insect releases
	Number	Number	Number
Parent	1,000,000	1,000,000	1,000,000
F_1	5,000,000	500,000	500,000
F_2	25,000,000	250,000	250,000
F_3	125,000,000	125,000	125,000 : 1,125,000 sterile
F_4	125,000,000	62,500	62,500 : 1,125,000 "
F_5	125,000,000	31,250	16,450 : 1,125,000 "
F_6	125,000,000	15,625	1,190 : 1,125,000 "
F_7	125,000,000	7,812	0

Obviously, if the strain of insects used for release were highly resistant to the insecticide, but the natural population was still highly susceptible, both systems could be employed simultaneously for maximum advantage. The application of an insect pathogen, or mass liberation of a parasite or predator that would destroy a high percentage of the immature stages, with the simultaneous release of sterile insects to compete with the normal adults, might be an effective and desirable combination. Mechanical destruction of the immature stages of an insect, such as the boll weevil (Anthonomus grandis Boheman) in squares on the ground, plus the simultaneous liberation of sterile adults in the cottonfields, would be representative of another combination that might be used to advantage without employing insecticides.

Regardless of the systems employed, the effects of a simultaneous integration of sterile-insect releases with other control methods within the same generation can have a dramatic impact on the insect population in a short time, and when the natural population is reduced substantially, the liberation of sterile insects alone probably would be the most economical way to achieve final elimination and to maintain control in areas subject to reinvasion of the pest by long-range migrants or by new accidental introductions.

Model 6 projects the theoretical effect of two systems of control, each 90 percent effective when carried out simultaneously for one generation, followed by the continued release of sterile insects only, in subsequent generations.

Model 6.—Trend of an insect population subjected to the combined use of sterile insects and a conventional system of control for one generation, followed by the release of sterile insects alone. All reproducing insects are assumed to result in a five-fold increase

Generation	Normal trend	Original population reduced by 90 percent	Fertile insects remaining	Sterile insects released	Insects reproducing
	Number	Number	Number	Number	Number
Parent	1,000,000	100,000	100,000	900,000	10,000
F_1	5,000,000	--	50,000	900,000	2,632
F_2	25,000,000	--	13,160	900,000	189
F_3	125,000,000	--	945	900,000	0

This model indicates the great potential of an integrated program consisting of conventional methods and the release of sterile insects. This becomes fully apparent only by carefully noting the theoretical effect of each system when employed alone. (Note models 2 and 3.) As previously shown, conventional control systems at the 90-percent level for each generation would require treatments for 18 generations when employed alone. The use of sterile insects alone would require the release of 45 million sterile insects during a period of five generations. However, by combining the two systems in a completely integrated program, theoretical elimination of the population would result from the application of conventional control methods plus 900,000 sterile insects for one generation, and the liberation of only 2,700,000 additional sterile insects for three more generations. The two systems might be regarded as synergistic in effect when combined for population control.

It is emphasized that the models established are hypothetical, but the writer feels that, in principle, they represent what we could achieve in practice. In order to put the basic principles into practical use against a given insect problem, details of the biology and behavior of the insect, the available methods of control, the relative costs involved in each system, and other factors must be considered.

We need to explore various new systems that will lend themselves to integration with the sterile-insect procedure. The use of insect pathogens against immature stages plus sterile-insect releases should hold much promise for the future. A combined system of mass production and liberation of parasites and predators when the population is high, gradually phasing into sterile-insect releases, conceivably could provide an excellent combination. These two systems have principles in common. Both methods would tend to become progressively more effective as the natural population declines. When the natural population of the host is high, there might be a substantial increase in the natural parasite population to augment the effects of those mass-produced and released. It is the writer's view, however, that when the host population reaches a low level, sterile insects will, for most species, be more efficient than parasites or predators. There is more and more interest in the development and use of attractants for male insects. The integration of male sex lures and sterile male releases should hold much promise. For example, if the males of an insect population are greatly reduced, and are replaced by sterile males, the required impact on the reproductive potential of the population can be achieved with fewer sterile insects.

Important new developments are being made in the insect attractant field. Effective means of attracting insects by chemical or physical means might offer the possibility of integrating the attractant and sterility principles without the necessity of rearing and releasing insects. The trapped insects might be sterilized and released, thus increasing the effectiveness of the trapping procedure.

It is hoped that the discussion up to this point will be helpful in giving the reader a better understanding of the principles and potentialities of the sterile-insect-release technique, particularly when integrated with other control methods. Suggestions for putting the sterility system into use for eliminating specific insects will be offered in another section of this report.

FACTORS TO CONSIDER IN APPRAISING THE FEASIBILITY OF EMPLOYING STERILE INSECTS FOR POPULATION CONTROL

A number of factors must be carefully analyzed in appraising the feasibility of using sterile insects for the control or elimination of established insect populations. There are circumstances where the method will not be practical, and this should be apparent after due consideration of all elements. On the other hand, there are circumstances where the method should be entirely practical, but for various reasons has not been so regarded by research workers.

The elements to consider will be discussed in some detail with the hope that such discussion will serve as a guide for investigators who may be familiar with the biology, ecology, and control of various insects, but who may not have carefully analyzed all of the factors having a bearing on the use of sterile insects for population control.

In some instances, extensive research on an insect may be necessary before even a reasonable estimate of the potential of the sterile technique can be made. In other instances, however, we now have enough information, if it is properly analyzed, to conclude whether or not research to develop the technique is justified.

Feasibility of Producing Sterility Without Producing Serious Adverse Effects on Mating Competitiveness

The sterile-insect-release technique requires that a method be developed for producing irreversible sterility in the insect to be released. Sterility of a type that destroys mating competitiveness will be of no value. The theoretical calculations in the various models included in this report, are based on the assumption that the males of the released organism are fully competitive. This is an assumption that may not be entirely valid for most insects.

Irradiated screw-worm flies (Cochliomyia hominivorax (Coquerel)) and tropical fruit flies, as examples, show some loss in competitiveness. The use of chemosterilants may result in less damage than radiation for many insects. However, if the competitiveness of the male organism released is reduced by one-half, for example, it would be necessary, theoretically, to release two sterile males to fully compete with each normal male. In other words, in the models previously considered, the release rate would have to be two times as high to produce the theoretical effect projected, assuming that all other elements are valid, as indicated. If the increase rate of an insect population were tenfold per generation and the sterile males released were only one-half competitive, it would be necessary to overflood the natural population with released insects at a ratio of 20 sterile to 1 nonsterile in order to expect a downward trend in the natural population. Such problems would not, in the opinion of the writer, invalidate the practicability of the sterile-insect procedure for many insects.

Research on materials and methods of producing sterility in insects has progressed substantially during recent years, and the probability is good that it will be possible to produce reasonably competitive sterile insects of any species for release. Depending on the sterility methods that may be developed, and through the selection of exceptionally competitive strains, it may be possible, for some species at least, to release insects that are even more competitive than the normal wild strain. Through selections carried out by A. H. Baumhover, of the Entomology Research Division, there is every indication that the strain of screw-worms employed in the eradication programs is more aggressive sexually than the original colony strain.

Two methods of achieving sterility (dominant, lethal effects in the genetic material) have been investigated most extensively. The use of X-rays or gamma rays from cobalt 60, as first investigated on the screw-worm by R. C. Bushland and D. E. Hopkins, and the use of chemicals for sterilization, as reported by G. C. LaBrecque and associates, are the sterility methods of most interest at present. However, these procedures may not necessarily be the only, or the best, ways of producing sterility for any given insect. Conceivably, hybrid sterility could be the preferred method for some insects, and hybrid vigor may actually result in more competitive insects. It is the writer's firm view that if other factors that determine the practicability of using sterile insects are favorable for any given insect species, difficulties encountered in preliminary efforts to achieve sterility without adverse effects on behavior should not deter research on the method. There is every reason to believe that it will be possible to develop satisfactory ways to achieve sterility in insects, in view of the progress that has already been made in the use of radiation, chemicals, or by crossing genetically incompatible varieties or strains of insects. Intensive research may be necessary (and would be fully justified for important insects) to achieve this objective, if all other factors appear favorable. The boll weevil seems to be one of the most difficult insects to sterilize without producing serious adverse effects on the competitiveness of the males, based on studies conducted by the Division entomologists located at College Station, Tex., and State College, Miss. There are, however, many elements in connection with the boll weevil problem (to be considered later) that would favor the sterility method for integration with other systems of control.

Practicability of Rearing or Collecting Organisms for Subsequent Sterilization and Release

Whether or not it will be practical to rear, or otherwise obtain, adequate numbers of an organism to control or eliminate a pest population is a question that can be determined only after careful consideration of a number of factors. As a general working hypothesis, it is submitted by the writer that where the complete elimination of a bisexual insect population is the final objective, and is feasible with current control procedures, there will be circumstances where final elimination can be brought about more effectively by the release of sterile insects, regardless of the cost of producing them. This generalization might also apply to vertebrate pests. At what stage the sterile-insect-release system will become useful will depend on the number of individual

organisms remaining in the environment, the number of sterile organisms required to achieve final elimination, and the relative cost of achieving elimination from a given population level by the available systems.

In appraising the feasibility of controlling or eliminating insect populations by the release of sterile organisms, we might regard the tsetse fly (Glossina spp.) as a good example of an insect problem to carefully analyze. On casual consideration, this group of related species in Africa might be ruled out for practical consideration of the sterile-release method, because of the inherently low reproductive potential of the flies, and the difficulties that can be anticipated in developing mass-rearing procedures. For this reason, these insects have been regarded by many as poor candidates for the practical application of the sterile-male-release method. The writer has studied this matter in some depth, and has prepared a special report on the subject, which was submitted to WHO for consideration. The conclusion reached was that, in spite of limitations imposed by the rearing factor, the method should prove to be highly favorable and entirely practical as the principle means for the elimination of the insects in most situations. If developed, the method should have advantages over current methods for the elimination of incipient tsetse infestations in areas of spread, as well as for low-level, established populations. The greatest value, however, should be derived by integrating sterile-insect releases with other methods of control. Hypothetical models were established and tested, which suggest that even if it costs as much as one dollar to rear or collect males for sterilization and release, their use would be more practical in some situations than the use of insecticides. If rearing or collecting costs within the range of 5 cents for each male could be realized, the use of sterile male tsetse flies should be advantageous under a wide range of circumstances. The manner in which sterile male tsetse releases might be employed will be considered further in another section of this report.

Entomologists and insect nutritionists have made outstanding progress during recent years in developing methods for the mass production of insects. With few exceptions, it seems safe to conclude that a determined research effort will lead to success in developing practical methods for rearing insects. We might include in such category heel flies (Hypoderma spp.), Japanese beetles (Popillia japonica Newman), or almost any insect that is different to rear, but which, in the final stages of an eradication effort, would require costly or undesirable treatments to destroy only a few insects. In considering this subject, we should not disregard the feasibility of rearing the organism on its natural hosts in sufficient numbers to be useful and practical in relation to costs for eliminating low-level populations of the pest by other means.

For most insects, it seems reasonable to conclude that methods can be developed for rearing insects in almost unlimited numbers. It then becomes a question of determining under what circumstances sterile-insect releases can be used to advantage over other systems of control, or integrated in a control program. The screw-worm was the first insect to be mass-produced for the sole purpose of utilizing the insects in a sterile-insect-release program. The cost of rearing screw-worms, for use in the eradication and control program in the southwestern United States, which is conducted jointly by the U.S. Department of Agriculture and the livestock industry, is less than $500 per million,

when fly production is at a rate of several billion a year. The Honolulu, Hawaii, and Mexico City tropical fruit fly laboratories of the Entomology Research Division, currently under the direction of L. F. Steiner and W. E. Stone, respectively, have made outstanding progress in developing procedures for rearing these insects by the millions or billions at a cost ranging from about $100 to $200 per million. Workers in other countries including Costa Rica, Israel, Greece, and Egypt are also making important contributions to mass-rearing procedures for tropical fruit flies.

The tobacco insects research laboratory of the Entomology Research Division, at Oxford, N.C., under the direction of F. R. Lawson, has made excellent progress in developing mass-production procedures for the tobacco hornworm (Protoparce sexta (Johannson)) that probably would fall within a cost range of $5,000 to $10,000 per million moths. Certain insects, such as Drosophila fruit flies, certain mosquitoes, the house fly (Musca domestica L.), the face fly (Musca autumnalis De Geer), and perhaps many crop pests could be mass-produced at costs that probably would be substantially less than $100 per million.

Investigators with the Entomology Research Division and cooperating State experiment stations have made excellent progress in the development of rearing methods for the production of virtually unlimited numbers of such insects as the pink bollworm (Pectinophora gossypiella (Saunders)), the boll weevil, codling moth (Carpocapsa pomonella (L.)), the European corn borer (Ostrinia nubilalis (Hübner)), the cabbage looper (Trichoplusia ni (Hübner)), the corn earworm (Heliothis zea (Boddie)), and other species that, even as late as 5 to 10 years ago, were regarded as difficult to rear under laboratory conditions. Basic studies on insect nutrition by Erma S. Vanderzant of the Division's cooperative cotton insects research laboratory at College Station, Tex., have contributed much to the progress on mass-rearing methods for a wide range of crop insects.

Necessity for Appraising Natural Population Density

With the possible exception of concern over mass-rearing procedures, the writer has gained the impression that most entomologists regard high natural population densities as the chief obstacle to successful application of the sterile-insects-release method. This is among the most vital of the factors to be considered in appraising the potential merits of the method. The dearth of quantitative information on natural insect population densities per unit area is really appalling. Information on actual numbers per acre, per square mile, per individual host tree, or any other unit of measure applicable to the pest involved, is absolutely necessary in order to make a reasonable approximation of the merits, or lack or merit, of the sterile-insects-release method. It is the writer's view that there is a general tendency for entomologists to overestimate the natural population density during periods of scarcity of the species. When precise information is lacking, and entomologists are asked to estimate the natural population density of the insects they are investigating, they tend to think of the situation when the

pest is most abundant, and disregard levels when the insect is least abundant. Another factor that seems to have been given little thought is a quantitative estimate of the population level that would remain in the environment after available methods of control have been applied. Research on the natural population density of various insects under different circumstances needs much more attention than has been given to it in the past. Until such information is available, especially for periods of scarcity, and after the use of stringent control measures for the insect under consideration, it will not be possible to make even a reasonable estimate of the role of the sterile-insects-release method in control or eradication efforts.

In attempts to appraise the sterility procedures, the writer has employed various ways to estimate a pest population. Examples of procedures followed in making such estimates may be helpful to others.

For one example, extensive information has been available for years on the percentage of cotton squares punctured by the boll weevil. Information has also been published indicating the number of squares boll weevils puncture each day. Cotton agronomists and entomologists have good information on the number of squares per plant and per acre at different fruiting stages. By considering such information, it was possible to estimate, with reasonable confidence, that a 5-percent square-infestation level at a given stage of fruiting would represent a certain number of boll weevils per acre. A reasonably reliable estimate of the number of insects present can be made at any infestation level and fruiting stage of cotton. By such means, the writer estimated that a typical overwintering population of boll weevils probably is about 200 insects per acre. In some areas one could expect this number to be exceeded, but in many areas the number of insects present could be expected to be substantially below this level. The second important factor was an estimate of the level of infestation that could be expected to occur during periods of scarcity after insecticides had been applied for boll weevil control. Although much information is available on the percentage of squares punctured, this had not been related to the number of insects remaining per unit area after the insecticides had been applied. However, the writer concluded, as early as 1958, that following a rather rigid program of insecticide use, the natural population should fall below 10 boll weevils per acre. There was also evidence that the rate of increase would range between 2.5- and 7.5-fold per generation. It was further judged that following a rigid insecticide program, the release of 100 to 200 reasonably competitive sterile male boll weevils per acre, per week, should provide an adequate ratio of sterile to fertile insects to force a further downward trend in the population.

Although successful methods for rearing boll weevils in the laboratory had not yet been developed, there was every reason to believe that even if rearing had to be done on cotton in artificially infested fields, it would be practical to produce and release several hundred boll weevils per acre, per week, at a cost readily competitive with the cost of applying insecticides each week. Accordingly, the writer advanced the hypothesis that the use of sterile male boll weevils could provide a more effective, a more economical, and a more desirable way to eliminate low-level populations than to employ insecticides for this purpose.

Entomologists with Federal and State research institutions have gained a great deal of precise information on the population dynamics of the boll weevil since 1958, which indicates that the original appraisal of the potential value of sterile male boll weevils was well within the realm of feasibility. Much additional research is needed, especially on methods of producing reasonably competitive sterile males. However, there is good reason to believe that sterile-male releases can eventually play a vital role in boll weevil eradication. The manner in which they might be used for highly effective population control will be considered in another section of the report.

The writer made similar studies to estimate the general magnitude of the population of hornworms on tobacco. In this instance, published data on the number of eggs deposited on tobacco plants during different times of the year were analyzed, the writer taking into account the number of tobacco plants per acre, and the egg-production potential of the moths. An estimate was made that for the spring brood, a moth population averaging about 40 per acre was fairly realistic. On the basis of research by tobacco insect workers, there was every reason to believe that it should be practical, through a coordinated cultural and/or insecticide program to reduce such a population to a level of about 8 moths per acre. On the basis of this level of moth density, and by taking into account the acreage of tobacco and tomatoes (the two principal host plants), the present costs for control, and losses caused by the pest, it was concluded that it would be practical to adequately overflood the natural population and obtain virtual elimination of hornworm populations, even if rearing costs for the moths were as high as 10 cents each. It appeared certain that through research it should be possible to develop methods of rearing the insect at a cost substantially less than this figure.

F. R. Lawson and associates of the Oxford, N.C. tobacco insects research laboratory have, during recent years, obtained a good quantitative estimate of the number of tobacco hornworm moths per acre of tobacco. Their data indicate that the rough estimate made by the procedure described was reasonably close, but probably a conservative estimate of the natural population density of the hornworm in the spring brood. Moreover, progress in research on rearing methods, conducted by the Oxford laboratory, indicates that the insect can be reared at a cost of less than 1 cent per moth, a figure one-tenth that regarded as practical in the original appraisal. Thus, through further research it should be possible to develop the sterile-insect method for controlling the tobacco hornworm population in the principal tobacco-growing areas at a cost which would be only a fraction of the current cost of control, plus losses. A more detailed appraisal of the potentialities of the method for tobacco hornworm control will be considered later.

Similar appraisals were made which suggested the feasibility of utilizing sterile-insect releases for controlling or eliminating such insects as the codling moth, pink bollworm, sugarcane borer (Diatraea saccharalis (F.)), and tsetse flies. As research advances on these and other species, it becomes evident that population densities of many insects are sufficiently low, or can be reduced to levels that will permit the use of sterile-insect releases as a final means for eradication or control.

We need more precise quantitative information on the natural population density, especially during periods of scarcity, for such insects as the tobacco budworm (Heliothis virescens (F.)), the corn earworm, cabbage looper, pink bollworm, the southwestern corn borer (Zeadiatraea grandiosella (Dyar)), house flies, and certain mosquitoes, just to name a few. Techniques such as the Lincoln index have been developed for making reasonably good estimates. Radio-tagged and released screw-worm flies were employed in early work conducted by R. C. Bushland, A. H. Baumhover, and their associates to obtain information on the natural population density of this insect. Various colored marking materials can be used to advantage. L. F. Steiner and associates of the Hawaii fruit fly laboratory have conducted much research on population density estimates of tropical fruit flies. By releasing a given number of marked flies, in a given area, over a certain period of time, and then determining the ratio of unmarked to marked insects recaptured in male lure traps, good estimates have been made. F. R. Lawson and associates have followed similar procedures in estimating the natural population density of the tobacco hornworm moth. Light traps were used for recapture of marked moths and for the capture of moths of the natural population. By employing such procedures it should be possible to make good estimates of the natural population density of many other insects.

Importance of Information on Current Losses and Current Control Costs in Estimating the Practicability of Rearing Insects for Release

In the final analysis, the practicability of utilizing a new method for complete population control of a pest will depend on the cost of such method in relation to current control costs, plus the losses caused by the pest, or its importance as a pest of man, or vector of human diseases. Consideration of these factors is essential in appraising the practicability of using the sterile-insect-release method, or any other method, for control or eradication. A few examples might be cited to emphasize this point.

Tsetse flies in Africa are of major importance as vectors of trypanosomiasis in livestock and man. Yet, based on the judgment of authorities in this field, economics will not justify eradication efforts in many areas. The current cost of eradication is too high in relation to the current economic returns that will accrue to agriculture to warrant eradication expenditures. The cost of methods now employed varies considerably in different situations, and constant improvements are being made. However, as a yardstick, the writer has used a cost figure of $500 per square mile as a reasonably valid estimate of current costs for eradication. Tsetse fly experts and economists in Africa consider this cost justifiable at present, from an agricultural viewpoint, in certain areas, but not in others. Any reasonable chance of reducing current eradication costs by using the sterile-release method would seem to justify a determined research effort. The relatively high current costs for tsetse fly eradication, and estimates of natural population densities of the insects in various situations, were the two major elements considered by the writer in appraising the possible role that sterile-male releases might play in tsetse fly eradication efforts.

As for many other insects, precise information is not available on natural population densities of tsetse fly species, although on the basis of general information, it can be assumed that for most areas the average density could be measured in terms of hundreds per square mile. On the basis of costs of current eradication methods for the tsetse fly, the first factor considered was the number of insects that it would be practical to rear for $500. By considering the wide variations in natural population density levels that may require treatment by current methods, and assuming that costs of applying insecticides, brush clearing, or other methods of control would remain reasonably constant, irrespective of population density, a cost figure of $1 per insect was judged to be practical, in relation to current control costs, for eliminating very low populations in some situations. However, it is believed that tsetse flies could be reared or collected at a much lower cost. Tsetse fly investigators have shown that pupae or adults can be collected from heavily infested areas at a cost substantially less than $1 per insect. It seems reasonable to assume that costs in Africa for rearing the insect can eventually be developed at a figure as low as 5 cents for each male, even for an insect having such a low reproductive potential as the tsetse fly. Various hypothetical models were then established and tested to estimate the effect of sterile male releases, taking into account available information on the biology and population dynamics of tsetse flies. As will be discussed in more detail later in this report, the writer concluded that tsetse flies should be included among the important insects that could be eradicated by the sterility method, especially in conjunction with limited use of insecticides to first reduce existing high adult populations to substantially lower levels.

By considering estimates of annual losses caused by a given insect, and costs for controlling it in relation to other elements that must be considered, it should be possible to make a reasonable estimate of the role of the sterile-insect technique in controlling or eradicating most of our major insect pests. Consider the codling moth, for example. It costs growers about $50 per acre each year to control the codling moth. For an insect that has such restricted hosts and obviously exists at a low-density level in commercial apple orchards intensively treated with insecticides, it would seem likely that the production of adequate numbers of codling moths for use in control would not be a major problem from a cost standpoint. If we assumed a cost figure of $5 per 1,000 for rearing and releasing codling moths on a mass-production basis, $50 would purchase 10,000 sterile insects and still be competitive in cost with insecticides. If the minimum cost of $1 per 1,000 moths could be achieved for rearing codling moths, it would be feasible to rear 50,000 sterile moths for use on each acre, each year. Although good data on natural population densities are not available, it seems obvious that the spring population of the insect in well-cared-for orchards will not exceed more than a few hundred moths per acre, and that it should be possible, without excessive cost, to further reduce the natural population, including populations from untreated domestic and wild host trees. Such appraisal suggested that the release of a few thousand sterile insects per acre should provide a high ratio of sterile to fertile moths. On the basis of this reasoning, the writer regards the codling moth a favorable candidate for control by the sterile-insect-release method. The eradication of codling moths from certain areas may be difficult, but an important factor to consider is that once an established population is under complete domination by sterile insects, but subject to reinfestation from

surrounding areas, it would no doubt be possible to maintain control year after year with far fewer insects than is required initially to achieve virtual elimination of the population.

Thus, even though it may not be possible to eradicate an insect population, the initial cost for bringing it under control by the use of sterile insects should not be the only factor to consider. The cost of a continuing sterile-insect-release program, in relation to the costs for the control methods now available, has to be considered. For the codling moth, continuing releases of sterile insects would no doubt be required in many areas to prevent reestablishment by migrant moths.

Research by Canadian entomologists on the sterile-insect method for codling moth control has been underway for a number of years under the direction of M. D. Proverbs. More recently, similar research was undertaken by B. A. Butts and M. A. Brunson of the Entomology Research Division. Encouraging results have been obtained. It appears that the chances are good for achieving success in the development of the sterile-insect procedure as a more economical, as well as a more desirable, way to control this key insect species than by the use of insecticides.

Other major insect pests, besides those discussed in some detail, should be favorable subjects for investigation. For many other insects, however, including some of our major pests, the chances of developing a practical way to use sterile-insect releases, do not seem favorable at the present time. If the pest has a wide host range, is present in large areas, has a high total population even at the lowest level in the seasonal cycle, can readily disperse into cultivated crops from an abundance of wild hosts, and the total economic loss is relatively low, it would seem desirable to concentrate on other methods of control.

Whether or not the sterile-insect-release method will have economic advantages over other methods of control for some of our major pests of agriculture is a debatable question. For example, the writer has considered the role that the sterile-insect-release method might have for controlling or eliminating the European corn borer. Investigators have developed good information on the population density of this insect. In view of the vast acreages of corn, the relatively low average loss per acre, and the relatively high overwintered populations, this insect is not, in the writer's opinion, among the major pests that could be controlled by the sterile-insect-release method. However, if some reasonably low-cost procedure could be developed to reduce the natural population to levels of the order of 100 moths per acre, the sterile-insect-release method might then become the best procedure to follow for maintaining complete control of the pest.

Mating Behavior a Factor in the Use of the Sterile-Insect-Release Method

When the sterile-insect-release method for population control was first employed, the general, but erroneous, concept was advanced that a monogamous mating habit by the insect was necessary for success. This belief still persists in the minds of many, so it

seems desirable to discuss this question to some extent. There is much that is not known about the effect of polygamy among insects, and the influence such a mating habit will have on the effectiveness of the sterility method. However, it can now be stated with assurance that a polygamous mating habit does not rule out the sterile-insect-release method as a practical approach to insect control and eradication. In fact, under certain circumstances, polygamy could be an advantage in the application of the method. There are several reasons why it is valid to conclude that polygamy is of no adverse consequence. The radiation method of producing sterility does not prevent the production of sperm in the male. This was determined by R. C. Bushland and D. E. Hopkins in their early work. They observed that eggs produced by normal females mated to irradiated males were fertilized but did not hatch. The radiation produces a dominant lethal effect. It has been shown by several investigators that chemosterilants, now under investigation, affect sperm in a similar manner. Thus, if we can assume that sperm in sterilized males are present in adequate numbers, and if they are reasonably competitive with sperm of normal males, we have a valid basis for assuming that polygamy is not an adverse factor.

We might establish a model in support of the hypothesis stated, by assuming that we have two types of insects—one that mates once only, and the other that mates an average of 10 times. If the sterile males in the population produce the same number of sperm, and if the sperm are fully competitive in the spermatheca of the female, the overall effect on the reproductive potential of the entire population will be the same. Note model 7.

Model 7.—The relative effect of sterile-insect releases on the reproductive potential of two hypothetical insect populations when one species is monogamous and the other is polygamous in mating behavior. It is assumed that both the sterile male insects and the sperm they produce are fully competitive with normal fertile males

Mating behavior	Number of insects in the total population		Percentage of females mating with sterile males	Percentage of sterile eggs in total population
	Sterile	Fertile		
Monogamous	90	10	90	90
Polygamous (average of 10 matings)	90	10	All females on average mate with 9 sterile males and 1 fertile male	On an average, 90 percent of the eggs are sterilized and 10 percent are fertile

Observations indicate that matings after the first, do not necessarily result in the deposition of sperm in the spermatheca of the female. This has been noted by investigators at the Hawaii Fruit Fly Investigations laboratory in Honolulu and by investigators of the Insects Affecting Man Investigations laboratory at Gainesville, Fla. There is good evidence that in some insects a single mating will fill the spermatheca with sperm, so that subsequent matings will not contribute to the sperm reserve. It may be the rule among polygamous insects that a relatively few matings will fill the sperm reservoir. Even if sperm from several matings are deposited in the reservoir, and if normal sperm and sperm carrying lethal factors mix in the reservoir, the final effect on a total population should be the same as single matings.

It has been observed by certain workers that the last mating among polygamous insects determines the source of the sperm that will fertilize eggs of the female. If this is the case, then a polygamous mating habit in an insect species can be an advantage. It would mean that sterile-insect releases can have an immediate adverse impact on the fertility of the adult population that is already present in the environment. For monogamous insects, such as the screw-worm, the presence of sterile males will not influence that part of the female population already mated. Thus, the monogamous mating habit is a great disadvantage when female insects outside of an area under treatment with sterile insects can mate with fertile males and then migrate into an area protected by sterile-insect releases. This is a major problem in the current screw-worm program in the Southwest. Females outside of the release zone in Mexico or Arizona may mate with fertile males and migrate for distances of 200 to 300 miles into the area of sterile-fly releases. If the insect were polygamous, and if matings with sterile males would nullify their prior fertile mating, the migrants would pose a lesser threat than they now do.

Up to the present time, sterile-insect releases have achieved eradication for both monogamous and polygamous insects—the screw-worm and the melon fly. The successful eradication of the melon fly from the Island of Rota through the cooperative efforts of the Entomology Research Division, the Department of the Navy, and the Trust Territories, demonstrated that an insect having polygamous mating habits could be eradicated by the sterile-insect-release method. There was no indication that polygamy was a deterrent in the eradication of the melon fly in this pilot eradication program.

Mating behavior, other than frequency of mating, could however be of great importance in limiting the effectiveness of sterile-insect releases. Probably, the most desirable characteristic is for the released males to disperse to a considerable extent in the search for females. Insects that are greatly restricted in their movement may pose problems of achieving distribution of the released insects in the numbers and places necessary to achieve the desired result throughout the infested area. This could pose a difficult problem in efforts to eliminate populations of the boll weevil by releasing sterile males. This insect, during the regular cotton-growing season, has rather restricted movement.

The behavior of the insect with respect to dispersion, as previously pointed out, could play a vital role in determining the effectiveness and practicability of using sterile insects. Although emphasis in the discussion has been placed on average population density per unit area and total population density in the entire area to be treated, the need for information on the distribution of insects within the area under control is of vital importance. It is known, for example, that the number of insects within the environment varies greatly for such insects as the screw-worm fly and tsetse flies. In the current screw-worm program, the rate of liberation may exceed 1,000 flies per square mile in known heavily infested environments, and as few as 200 per square mile in areas of low density.

The chances for effective utilization of sterile insects probably are best for those species that tend to disperse to a considerable extent. Insects that have a greatly restricted range of movement may pose problems of achieving adequate distribution and placement of sterile insects in the required number to satisfactorily compete with the number of normal insects in different parts of the total area. For example, in attempting to control or eradicate scale insects by releasing sterile insects, we could anticipate difficulty in achieving adequate distribution of the released insects even on a single tree. In order to achieve complete population control of an insect, it is important that all segments of the population are adequately overflooded with sterile insects.

In experiments to test the ability of sterile insects to achieve complete population control, it is essential that the population be completely isolated from the insect in surrounding areas. If the test area is within flight range of adult females that may have mated with fertile males outside of the release area, complete elimination cannot be demonstrated. Moreover, the released insects that move out of the area will reduce the impact on the natural population within the area. Failure to demonstrate eradication of the screw-worm on the Island of Sanibel, 2 miles off the west coast of Florida, even though the density of the natural population declined rapidly after sterile-male releases were started, led to the decision to conduct further pilot eradication tests on the Island of Curaçao, to which, it was believed, screw-worm flies could not migrate from the South American mainland—a distance of about 50 miles.

Tropical fruit flies are known to be long-range migrants. Fruit fly investigations by the Hawaii fruit fly laboratory on the Island of Rota, which is about 35 miles from Guam, made it possible with available research resources to conduct valid eradication tests involving both the melon fly and the oriental fruit fly, but even here there is evidence that some flies will succeed in crossing the 35-mile water barrier.

On the basis of current knowledge of the flight range of the screw-worm fly, a valid eradication experiment could not have been conducted in an area of less than 40,000 square miles, and it probably would have required an area of 100,000 square miles.

Research resources are never adequate to conduct tests of such size. It is known by flight-range tests recently conducted by workers at the Mission, Tex. screw-worm plant that the insect will fly 180 miles, and there is evidence from screw-worm case incidences that some migration up to 300 miles occurs. If the importance of the factor of isolation had not been properly appraised in connection with early experiments to test the principle of screw-worm eradication by sterile-insect releases, it is almost certain that the sterile-male method could not have been demonstrated as a practical way to eliminate or control populations of this important pest.

It is the writer's view that entomologists, generally, have the tendency to underestimate the distance that insects will spread, and consequently, may not properly appraise the importance of migrating insects in judging the potential value of various control or eradication methods, such as sterile-insect releases, chemical attractants, light traps, or even insecticides. The writer urges that research workers give due consideration to the establishment of proper test procedures to evaluate the impact of control measures on the total population of an insect, whether the method involves the use of sterile insects, or some other system. Experiments to test eradication procedures should be conducted on isolated populations of the insect.

Release of Strains Adapted to the Natural Environment

Another factor that may be of major importance in achieving the maximum effect of sterile-insect releases is the adaptability of the strain to the environment where releases are to be made. There is considerable evidence that insects reared under laboratory conditions for many generations undergo changes in behavior that may adversely affect their ability to survive and compete satisfactorily with the wild strain in the natural environment in which they are to be released. It is likely that most laboratory strains of insects possess certain behavioral characteristics resulting from natural selection in captivity that could handicap their survival in nature. The Gainesville, Fla. laboratory of the Entomology Research Division undertook a pilot experiment some years ago to determine whether a natural population of the common malaria mosquito (Anopheles quadrimaculatus Say) could be brought under control in a semi-isolated area by the release of gamma-irradiated males. The experiment proved unsuccessful. Subsequent laboratory and field studies indicated that the laboratory strain, reared in captivity for 25 years or longer and through perhaps 200 or more generations, did not readily compete with normal wild males in mating with wild females. This example of failure in the application of the sterile-male-release method cannot be ascribed to a defective principle but rather to the release of a strain inferior to the wild one from the standpoint of competitiveness in the field.

Many investigators have reported difficulty in establishing new colonies of an insect species that would thrive in the laboratory even though their laboratory-adapted strain was simultaneously developing well under the same conditions.

It is possible, too, that the environmental conditions under which insects are mass-produced will adversely affect their vigor and competitiveness when released in a more stringent natural environment.

Obviously, there is much that we do not know about the competitiveness of insects reared under laboratory conditions and released into the natural environment. Changes in behavior or vigor that develop in laboratory strains may affect their competitiveness in the field and be independent of any adverse effects of radiation or chemosterilant treatment. The behavior of laboratory-reared insects after release compared with the behavior of the wild population may be one of the vital aspects for investigation in developing the sterile-insect-release method for a given pest. Population geneticists may be in a position to contribute materially in this field. Through selection, under proper artificial environmental conditions, it may be possible to maintain field adaptability and competitiveness in strains that are to be employed for release, or even to develop strains that are better adapted and more competitive in a given environment than the wild strain. For example, the screw-worm research group at Mission, Tex., under the direction of A. H. Baumhover, obtained encouraging laboratory results in selecting a screw-worm strain that appears to be particularly resistant to starvation (food and water) during the first few days after emergence from the pupal stage.

Summary of Basic Requirements and Factors That Determine the Feasibility of Employing the Sterile-Insect-Release Technique

a. Availability of a method of inducing sterility without serious adverse effects on mating behavior and competitiveness.

b. Method of rearing the insect.

c. Quantitative information on natural population density at the low level in the population cycle.

d. A practical way of reducing natural populations to levels manageable with sterile insects.

e. Information on rate of population increase as a guide for determining the necessary rate of overflooding with sterile insects.

f. Cost of current methods of control plus losses caused by the insect must be higher than the cost of reducing the natural population plus the cost for rearing and releasing the required number of sterile insects.

g. If complete population control cannot be maintained because of reinfestations by migrating insects, or new introductions, the cost of maintaining complete control by continuing sterile-insect releases must be favorable in relation to the costs for current methods of control, plus additional losses caused by the insect.

h. There would be justification for employing the sterile-insect-release method, even if it were more costly than current ways to control or eradicate insect populations, if it provides advantages in overcoming hazards to man and his environment.

i. Sterile insects to be released must not cause undue losses to crops or livestock, or create hazards for man that outweigh the benefits of achieving or maintaining population control.

HOW STERILE INSECTS MIGHT BE EMPLOYED TO CONTROL POPULATIONS OF CERTAIN SPECIES

The foregoing discussion considers the principles involved, and the factors that will determine the role of sterile insects in controlling insect populations. Every insect problem requires a detailed analysis of the many factors already alluded to that have a bearing on the method, and much research will be needed to develop the technique for practical use. However, it might be helpful to consider specific insect problems and, with the aid of hypothetical models, indicate how populations of these insects might be controlled or eliminated by making sterile-insect releases. The writer has conducted special studies on a number of important insects that have widely varying habits, in efforts to appraise the role that sterile-insect releases might have in their control or elimination. The insects considered include the boll weevil, the tobacco hornworm, and tsetse flies. Factors considered and procedures followed in making appraisals will be discussed in detail. There is no assurance that success will be achieved by the use of the sterile-insect technique for these insects. However, on the basis of present concepts, the writer believes that there is an excellent chance that the technique can play a major role in eliminating or controlling populations of all three species. It might be stated that a similar appraisal of the potential for the sterile-male method was made for eradicating screw-worm populations long before the effectiveness and practicability of the method was established. A vast amount of research by such able scientists as R. C. Bushland, A. W. Lindquist, A. H. Baumhover, C. H. Husman, and others was required to develop the techniques, and improvements are constantly being made by research and control workers. However, practical experience has fully confirmed the hypotheses originally established.

Boll Weevil

The boll weevil is among the most destructive of the insect pests in the United States. Annual losses to cotton growers are estimated to average about $300 million. In addition, growers spend an estimated $70 million each year to prevent even higher losses. About 10 million acres of cotton are grown in areas infested by the pest. Cotton is the chief host for the insect, and entomologists generally assume that the boll weevil

could not survive if it were not permitted to develop on cotton. The boll weevil is a key species on cotton. Except for early stalk destruction in limited areas, insecticides now provide the only effective way to achieve control. The necessity for using insecticides to control this insect complicates the control of other cotton pests, including the bollworm complex (Heliothis spp.), spider mites, and aphids. In view of the extensive losses caused by the insect, the adverse effects of insecticides on beneficial insect parasites and predators and on pollinating insects, and the large amount of insecticides that are applied in the environment in connection with its control, the Entomology Research Division has oriented its research program to develop a method, or combination of methods, that can be employed to eliminate the insect from the United States.

Because of the extensive losses that it causes, and the growing concern over the side effects produced by the insecticides employed each year for its control, it is apparent that it would be profitable to the cotton industry and to the Nation as a whole to invest large sums of money to achieve complete elimination of the boll weevil.

Significant Features About the Boll Weevil That Have a Bearing on the Feasibility of Employing Sterile Insects for Population Control

The total number of boll weevils in the infested areas, even during their periods of greatest scarcity, is very large. Nevertheless, after extensive analysis of the boll weevil problem, it has long been the view of the writer that the population density per unit area is relatively low in comparison with many other economic pests. There is good evidence that the initial population of the insect in the spring, after hibernation, can be expected to average about 200 boll weevils per acre. Much of the acreage could be expected to have higher populations, but there is probably more acreage where the population would average substantially less than 100 per acre. Reasonably effective methods of chemical control have been developed through intensive research by State experiment stations, Federal research institutions, and industry. Cultural control methods are useful in limited areas. Thus, it is possible, and practical, to reduce the population to low levels per unit area. This was demonstrated in early research with chlorinated hydrocarbon insecticides by K. P. Ewing[2/] and C. R. Parencia of the Entomology Research Division. It is common practice, as a result of their work and that of entomologists with various other Federal and State laboratories, for farmers to employ about four insecticide treatments when the insect is emerging from hibernation to reduce the overwintered population. Such treatments, properly timed, probably reduce the surviving, overwintered population by 90 percent. More recent studies by the Entomology Research Division have been conducted for the purpose of determining as precisely as possible the extent of reduction that is feasible and practical in the spring by applying about six properly timed treatments. These studies, conducted in the vicinity of Tallulah, La., and Florence, S. C., indicate that the spring population can be reduced by 95 percent or more. Thus, an intensive spring-treatment program can be expected to reduce the population to an average of about 10 or less boll weevils per acre.

2/ Retired.

As a result of basic studies on the diapause phenomenon in the boll weevil by J. R. Brazzel and L. D. Newsom of Louisiana State University, prehibernation control has been given more attention. Cooperative research by Texas A. & M. College and the Entomology Research Division, which was carried out by J. R. Brazzel and T. B. Davich, has shown that about four properly timed insecticide treatments in the fall can also be expected to reduce the prehibernating population by about 90 percent. The writer has estimated (unpublished report) that by applying about seven insecticide treatments, properly timed to provide maximum kill of both reproducing and diapausing boll weevils in the fall season, the hibernating population could probably be reduced by 95 percent or more. Results of field experiments conducted by investigators at the boll weevil research laboratory at Stoneville, Miss. indicate that this is a conservative estimate. It is believed, therefore, that by combining a fall- and a spring-treatment program, it would be economically feasible to reduce a normal population to less than one boll weevil per acre. The combined effect of two separate control programs, each 95-percent effective, would theoretically reduce the population by 99.75 percent, or one boll weevil on two acres of cotton, if 200 boll weevils per acre is representative of a normal, uncontrolled, spring population.

In an unpublished report on the population dynamics and control of the boll weevil prepared in 1959, the writer advanced the hypothesis that 95-percent control of prehibernating boll weevils in the fall, and a similar degree of control in the spring, should virtually eliminate populations of the pest in many situations. As research advances, this appraisal seems more and more realistic. At least it seems reasonable to believe that it would be possible and practical, with available materials and methods, to reduce boll weevil populations to levels of a few insects per acre. In such event, an overwhelming ratio of sterile to fertile insects could be achieved by releasing only a few hundred sterile insects per acre.

A field experiment is underway by T. B. Davich and M. E. Merkl of the Boll Weevil Research Laboratory at State College, Miss., to determine to what extent a boll weevil population can be reduced by an intensive and combined fall and spring insecticide-treatment regime. Such effort has never been made to determine, on an isolated population, what effect such a combined program will have on the total population. Even if the estimated 95-percent levels of control cannot be achieved under operational conditions by each of the two series of treatments, it is believed that at least 90-percent control of the population can be achieved by an insecticide-treatment regime in the fall and a like percentage in the spring. This would reduce the population by 99 percent during the period of greatest scarcity for the insect. If 200 boll weevils per acre is representative of a normal surviving spring population, 99-percent control should reduce the number to two boll weevils per acre. The elimination of such low-level populations by further use of insecticides would probably require at least as many treatments as were required to eliminate the first 99 percent. However, the sterile-insect-release method, if perfected, should provide a more economical and more desirable method for final elimination of such low populations. This line of reasoning has been the basis for the writer's proposal that the sterile-insect technique could play an important role in boll weevil eradication.

If we can safely assume that the attainment of a population level averaging two boll weevils per acre (one male and one female) is within the range of practicability with current control methods, the total boll weevil population for final elimination would be of the order of 20 million boll weevils (10 million males and 10 million females). Then, if we assume that an initial ratio of 100 or even 200 reasonably competitive sterile males to 1 fertile male would be required to assure a further downward trend in the population, we would have a highly promising system for final elimination of the population. It is the writer's view that no insect species under field conditions could continue to maintain its population level if subjected to such high ratios of reasonably competitive, sterile insects. In order to achieve ratios of 200 sterile to 1 fertile boll weevil during the first generation after treatment with insecticides, the production of 2 billion male boll weevils for use on 10 million acres would probably be required. Additional releases at the original level for two more generations would require the production of a total of 6 billion males or a total of 12 billion of both sexes. Theoretically, eradication should be achieved with a high safety margin. This many insects, on casual analysis, may seem to be a staggering number, but in comparison with the costs for a full-season, chemical-control program that would theoretically be necessary to eliminate such a low population, the cost for producing 12 billion boll weevils should be very low.

Excellent progress, as the result of research by various laboratories of the Entomology Research Division and State agricultural experiment stations, has been made in developing ways to rear the insect in the laboratory. Research on mass-production procedures is being carried out by R. T. Gast at the Boll Weevil Research Laboratory at State College, Miss. Mass-rearing methods need to be perfected, but it is believed that the insect could be mass-produced at a cost of $5,000 per million males, and possibly for less. If 6 billion males were needed for final elimination of a low-level population, the cost of producing the sterile insects would be of the order of $30 million for use on 10 million acres of cotton, which would amount to only $3 per acre. This would be a nominal sum in relation to a cost of $20 or more per acre for 10 to 12 treatments with insecticides, but such insecticide treatments alone, theoretically, would not be as effective as sterile males for eliminating a population, even after it had been previously reduced as low as two boll weevils per acre.

The above appears to be a reasonably accurate estimate of the number of insects that would have to be dealt with following an intensive insecticide-control regime, both in the fall and spring. The low-population level that seems to be attainable should fall well within the range that could be managed by the sterility technique, if reasonably competitive males can be produced.

Ways of sterilizing the boll weevil without serious adverse effects on competitiveness of the males have not yet been achieved, as mentioned earlier in this publication, but investigations are continuing at the Boll Weevil Research Laboratory. In spite of the adverse effects on mating competitiveness resulting from current methods of producing sterility, D. A. Lindquist and associates of the Division's laboratory at College Station, Tex., and T. B. Davich and associates of the Boll Weevil Research Laboratory at

State College, Miss., have demonstrated that sterile male boll weevils under cage and field conditions do exert a depressing effect on the reproductive potential of normal populations, and the elimination of low-level isolated populations has been achieved by high ratios of sterile to fertile males.

The foregoing discussion considers the role that sterile male boll weevils might play in eradication, if it is necessary to reduce the natural population to the maximum extent possible before using sterile insects. However, it is the writer's view that sterile male boll weevils might be employed more efficiently if their use is properly integrated with a minimum number of insecticide applications. Based on studies of various hypothetical models, it is estimated that the use of reasonably competitive, sterile, male boll weevils would be the most economical, and no doubt also the most desirable, way to eliminate populations when the natural population has been reduced to the order of 10 insects per acre.

There are several ways, theoretically, whereby the use of insecticide treatments and sterile male boll weevils could be integrated to achieve total population control. A number of possibilities have been studied, but the system that seems especially encouraging is to reduce the overwintered population by inaugurating an intensive insecticide program, either in the fall or spring, and then to release sterile insects. If sterile boll weevils, mating with boll weevils emerging in the spring, would preempt other matings, an insecticide program in the fall should be satisfactory. If treatments were made in the fall, sterile males would be released at squaring time, possibly after one insecticide treatment. An intensive cultural program in the fall and through the winter, followed by the release of sterile males, might be the most desirable procedure for study in south Texas.

As discussed earlier, it seems that an adequate number of properly timed insecticide treatments during the spring period could be expected to reduce the overwintered population by 95 percent. For the purposes of this report, a spring treatment program, followed by the release of sterile males, will be considered. A proposed integrated program of insecticide applications and sterile male releases is shown in model 8. The model assumes six insecticide treatments at 5-day intervals in the spring, beginning when the first squares appear, in order to reduce the population, as well as reproduction in the parent generation, by 95 percent. We could expect a normal, uncontrolled parent population of 200 boll weevils per acre to increase to 1,000 per acre for the F_1 generation. This would amount to an average emergence rate of 50 boll weevils per day during the F_1 emergence period. But, if we assume 95-percent control of reproduction by virtue of the insecticide treatments, we could then assume an accumulative total of only 50 boll weevils in the F_1 generation, or an average of 2.5 per day.

It is proposed that 300 sterile males be released after the last of the six applications of insecticides, and maintained at that level for the 20-day F_1 emergence period. The ratio of sterile to fertile insects can be expected to be higher during the early part of the F_1 emergence period than near the termination because of the accumulation of normal males during this 20-day period.

Model 8.—Hypothetical model showing the potential effect of sterile male boll weevils competing with the emerging F_1 and F_2 fertile populations. The model assumes 95-percent reduction of a normal parent population of 200 boll weevils per acre by the use of six insecticide applications prior to the release of 300 sterile males per acre. A five-fold increase rate of survivors from the parent to the F_1 generation, and a uniform daily emergence rate for the 20-day F_1 emergence period are assumed. Another insecticide application is made at the termination of the F_1 emergence period, and sterile males are then maintained at the rate of 200 per acre in the F_2 generation until the population is eliminated

Boll weevil population	Parent generation	F_1 accumulative emergence rate					F_2 accumulative total	F_3 accumulative total
	Boll weevils per acre	1 day	5 days	10 days	15 days	20 days		
	Number	Number	Number	Number	Number	Total	Number	Number
Uncontrolled population	100 males	25	125	250	375	500	2,500	12,500
	100 females	25	125	250	375	500	2,500	12,500
Reproducing population under treatment with insecticides	5 males	1.25	6.25	12.5	18.75	25[1/]	5[3/]	
	5 females	1.25	6.25	12.5	18.75	25	5	0
Fully competitive sterile males	300 per acre maintained during F_1 emergence period.						200 during F_2 emergence period	
Ratio—sterile / fertile [2/]		240 / 1	48 / 1	24 / 1	16 / 1	12 / 1	80 / 1	0

1/ A nonresidual insecticide application is made on the 20th day to destroy accumulated F_1 boll weevils.

2/ During the F_1 generation the average ratio of sterile to fertile insects would be 24:1, representing 90-percent control of reproduction; during the F_2 generation, 80:1, representing further control of 98.8 percent.

3/ With a calculated minimum ratio of 40:1 and an average of 80:1 for the F_2 period, no fertile matings would be expected.

Model 8 shows the calculated ratio on the first day during the F_1 emergence period, and on the 5th, 10th, 15th, and 20th days. It is assumed that the rate of emergence is constant, although considerable variation would no doubt occur in actual field populations. The sterile male population is also assumed to be constant at a level of 300 per acre.

It should be noted that the theoretical ratio of sterile to fertile insects would be 240:1 on the first day after treatment, and 12:1 by the 20th day, if the sterile male population is maintained at 300 per acre. No mortality is calculated for either the naturally emerging population or the released males. Theoretically, reproduction would be reduced by more than 99 percent on the first day and 92 percent on the 20th day. The average ratio of sterile to fertile insects would be 24:1, which would represent a 96-percent overall control of reproduction. Actually, the theoretical effect would be slightly higher, if we allowed for a 3-day preoviposition period, which was not done in the model. The use of such a regime of sterile males would seem to take full advantage of the biology and population dynamics of the insect. The impact of 96-percent control of reproduction during the F_1 period should be substantial, even allowing for a five-fold increase rate for those that reproduced successfully during this period. If only 4 percent of the F_1 population of 50 boll weevils reproduced successfully, and these produced five times the number of progeny, the total F_2 natural population would be 10 per acre.

If the F_2 boll weevils emerged uniformly during the 20-day period, this would mean a daily emergence of 0.5 boll weevil per day. However, the boll weevils accumulating during the F_1 period could overlap the F_2 generation. Theoretically, sufficient numbers of fertile males would accumulate by the end of the F_1 emergence period to reduce the sterile to fertile ratio to 12:1. It would seem advantageous, therefore, to employ one additional insecticide treatment on the last day of the F_1 emergence period to destroy all adults, both fertile and sterile, and immediately release more sterile males to compete only with the emerging F_2 boll weevils. In this model, a projected release of 200 sterile males per acre would theoretically be adequate to assure no reproduction of the few F_2 emerging boll weevils. According to the model, the average ratio of sterile to fertile insects would be 80:1 during the F_2 emergence period. The maximum ratio would be 800:1 on the first day of the F_2 emergence period, and the minimum would be 40:1 on the last day. No reproduction would be expected during the F_2 generation, and theoretical elimination would be achieved on the basis of the populations on 1 acre of cotton.

Model 9 projects the estimates for a representative population on 1,000 acres of cotton using the basic information developed in model 8. Model 9 also includes the estimated trend of a normal, untreated population and a population subjected to a full-season program of insecticide treatments only. It is assumed that insecticide treatments directed against the F_2 and F_3 generations will be only 90 percent effective instead of 95 percent, as projected for the overwintered population. It is generally agreed by entomologists that as cotton grows larger it becomes more difficult to achieve levels of control comparable to those obtained when the cotton is smaller. It is possible, too, that the increase rate is higher during the F_2 and F_3 generations because infested squares are less subjected to desiccation by direct sunshine.

Model 9.—Hypothetical model showing the trends of a boll weevil population on 1,000 acres of cotton when subjected to: (1) No treatments; (2) full-season treatments with insecticides; (3) an integrated insecticide-sterile insect program. The model assumes a five-fold increase rate per generation for all surviving boll weevils that reproduce

Boll weevil population	Parent generation	F_1 generation	F_2 generation	F_3 generation
	Total boll weevils on 1,000 acres	Total boll weevils (reproducing)	Total boll weevils (reproducing)	Total boll weevils (reproducing)
	Number	Number	Number	Number
1. Uncontrolled population	100,000 males 100,000 females	500,000 males 500,000 females	2,500,000 males 2,500,000 females	12,500,000 males 12,500,000 females
2. Population control—led by insecticides only 1/	5,000 males 5,000 females	2,500 males 2,500 females	1,250 males 1,250 females	625 males 625 females
Control	95 percent	90 percent	90 percent	90 percent
3. Population control—led by insecticides in parent generation; sterile males in F_1, F_2, and F_3 generations; plus one application of insecticides on the 20th day of the F_1 period	Normal boll weevils Sterile boll weevils	25,000 males 25,000 females 300,000 males	5,000 males 5,000 females 200,000 males	300 males 300 females 100,000 males
Control (theoretical)	95 percent	96 percent	98.8 percent	99.7 percent

1/ Insecticides destroy and control reproduction of 95 percent of parent population and 90 percent of F_1, F_2, and F_3 progeny.

A rigid program of insecticide treatments would not, according to the assumptions, achieve eradication, although the population would be reduced to an average of about 1 boll weevil per acre in the F_3 generation. Failure to show elimination of a population by the use of insecticides alone is reportedly in agreement with general observations in practical control of boll weevils during the regular growing season. To the writer's knowledge, however, no full-season insecticide program of the type projected in the model has ever been carried out against a completely isolated boll weevil population.

In contrast with the calculated effect of using an insecticide program alone, the population subjected to sterile males instead of insecticides in the F_1, F_2, and F_3 generations, shows a dramatic decline, and theoretical eradication of the population is achieved in the F_3 generation by a wide safety margin.

The writer recognizes that it is not yet possible to produce fully competitive sterile males, but if sterile males eventually can be produced that are even one-third to one-half competitive, it should be possible to eliminate a low-level population—about 10 or less per acre—within three generations by using a total of about 1,000 sterile males per acre. If this can be achieved, the sterile-insects technique will be a highly economical method for boll weevil eradication when considered in relation to current costs for control and losses that occur in spite of control efforts.

Cost Analysis

It may be appropriate to make a cost analysis of the two systems of control projected in model 9. The full-season insecticide regime, as projected, would require 18 treatments. At a cost of $2 per treatment, the total per-acre cost would be $36. Theoretically, however, complete population control would not be achieved. It is not uncommon for cotton growers under current practices to apply 18 treatments each season for boll weevil control.

The integrated sterile-insect-release and insecticide program, theoretically, would require 7 insecticide treatments and enough sterile male boll weevils to maintain an average population of 300 per acre during the F_1 generation, 200 per acre during the F_2 generation, and 100 per acre during the F_3 generation. If we assumed that 1,000 sterile males actually would be required, and if $5 per 1,000 would be a reasonable estimate for the mass production and release of this insect, the total material and application cost for eliminating boll weevil populations would be $19 per acre. Many growers exceed this sum each year merely for boll weevil control using current methods.

To project the cost analysis even further, an average cost of $19 per acre on 10 million acres would amount to $190 million. This would not include any other costs of an operational program. This estimate is purely hypothetical because all of the projections are hypothetical. Nevertheless, the potential possibilities are projected on the basis of a conservative analysis of the boll weevil problem in relation to the potentialities of the sterility principle. A fully integrated program of insecticides and sterile

male releases more effective than the procedure outlined above might be developed. Preliminary calculations indicate that the use of nonresidual insecticide treatments interspersed with the release of sterile males would be the most efficient integrated program. Such a program would take full advantage of the biology and mating behavior of the insect. In such integrated programs the development and use of a strain resistant to the insecticide employed would be a great advantage over a normal susceptible strain. The writer believes that there is every reason to regard the sterile male method as a feasible approach to boll weevil eradication. Any measure that conceivably could achieve eradication of a pest at a cost less than the annual losses, would seem to justify adequate research effort by scientists.

Tobacco Hornworm

Significant Features of the Insect That Have a Bearing on the Possible Use of Sterile Insects for Population Control

The tobacco hornworm (Protoparce sexta (Johannson)) and the tomato hornworm (Protoparce quinquemaculata (Haworth)) are major pests of tobacco and tomatoes. For the purpose of this report, only the tobacco hornworm, the more important and the more abundant of the two species, will be considered, although both species would have to be dealt with in any effort to protect tobacco from hornworms. Losses caused by tobacco hornworms on tobacco are estimated to be about $35,000,000 annually. The amount spent for their control by tobacco growers is difficult to estimate, but would probably amount to $10,000,000 annually.

The total acreage of tobacco and tomatoes east of the Mississippi River amounts to about 1,250,000 acres. As mentioned elsewhere in this report, the writer has estimated the natural population density for the spring brood to be of the order of 40 moths per acre. Based on actual field data obtained by F. R. Lawson and his associates of the Oxford, N.C. laboratory, this estimate is probably high. To be conservative, however, the basic population will be considered to be 40 moths per acre. Lawson and associates estimate that through a fully coordinated fall program, based largely on cultural control practices, it should be feasible to reduce the normal population by 80 percent. According to the basic assumption, this would mean an average of about 8 moths per acre for the spring brood, following the previous fall cultural program. If 8 moths per acre of host crops is a valid estimate, the total spring brood of moths would consist of about 10,000,000 moths.

If we assume that a population of hornworms under normal tobacco-growing practices will increase at a five-fold rate per generation, it would be necessary to overflood the natural population by more than 4 to 1 to start a downward population trend. A 10:1 ratio will be established as the initial release rate. This would require 100 million moths for the first brood.

If the cost of rearing moths is calculated at $5,000 per million, the total cost for moths for brood 1 would be $500,000. It is assumed that the same number of moths would be required for brood 2.

Assuming that the theoretical effects are achieved during the first year, the number of moths required for the second year could be reduced by one-half and still achieve complete domination of the population. A mortality of 75 percent is assumed for the population entering hibernation during the first winter after the program is initiated.

The calculated trend of the hornworm population subjected to the 2-year program as outlined, is shown in model 10. Theoretical elimination of the population would be achieved by the end of the second season.

Model 10.—Estimated trend of the hornworm population east of the Mississippi River when subjected to sterile-moth releases in a 2-year program. An increase rate of five fold for each brood is assumed for a normal population. Sterile insects are assumed to be fully competitive. Following a rigid cultural program in the fall, the initial spring population is assumed to be 8 moths per acre on 1,250,000 acres of tobacco and tomatoes, making a total of 10,000,000 moths in the total population at the start

Broods	Natural moth population	Sterile moth population	Ratio of sterile to fertile moths	Number of moths reproducing
First year				
1	10,000,000	100,000,000	10:1	909,090
2	4,545,450	100,000,000	22:1	197,454
Second year				
1	246,818 1/	50,000,000	202:1	1,215
2	6,075	50,000,000	8,230:1	0

1/ A mortality of 75 percent owing to hazards during hibernation was assumed. Theoretically, a moth population of 987,270 would have resulted from the 197,454 reproducing moths in the second brood in the absence of winter hazards.

It is not possible to make an accurate estimate of the cost for a program of the type projected. However, the cost for producing a total of 300,000,000 moths would probably amount to about $1,500,000. If all other costs for such a program were equivalent to the cost for rearing moths, the overall costs would be $3,000,000 to achieve complete domination and elimination of the original established population.

In all probability some moths would have to be released each year in a continuing program to prevent reestablishment of long-range migrants from other areas. Such maintenance programs should, however, cost much less than the yearly operations during the first 2 years, which are designed to achieve complete control over the original population.

Again, these projections for controlling the tobacco hornworm are mere estimates based on a hypothetical situation. There is reason to believe, however, that they reasonably reflect what could be achieved in the application of this technique, once fully developed and perfected. If the estimates are reasonably valid, the total program would cost less than the expenditures for controlling the insect each year, but in addition all losses caused by the pest should be eliminated completely.

Tsetse Flies

In appraising the sterility principle for controlling or eradicating tsetse flies, advantage has been taken of every opportunity to review literature and discuss tsetse fly biology, ecology, and behavior with experts in the field.

Scientists working on tsetse flies have obtained much valuable basic information on the biology, habits, ecology, and population dynamics of the various species in Africa. Additional information is needed, however, on pertinent aspects of the biology, ecology, behavior, dispersion, and population densities of the various species in relation to the sterile-insect-release technique before a full appraisal can be made of the potential value of the method. Information is needed on ways to produce sterility in various species. Methods of rearing, or efficient methods of trapping the insects must be developed. However, the writer is confident that the sterility method offers a procedure that can be developed so that it will be of great value in tsetse fly control and eradication programs.

The same general approach in estimating the value of the sterile-insect-release technique for other insects has been followed in appraising the sterile-male method for tsetse fly control or eradication.

In making this appraisal, the writer has drawn heavily on the compilation by Buxton, which discusses almost every aspect of the biology, ecology, and control of the tsetse flies. The writer also wishes to acknowledge, with appreciation, the opportunity to discuss, or communicate on, matters of tsetse fly biology, ecology, behavior, rearing methods, and current control procedures with such authorities as J. Ford and his associates of the Department of Veterinary Services, Federation of Rhodesia and Nyasaland, Salisbury; W. H. Potts, Commonwealth Bureau of Entomology, London, England; P. E. Glover and W. P. Langridge, Kenya Veterinary Department, Kabeta; K. S. Hocking, Tropical Pesticides Research Institute, Arusha, Tanganyika; and J. P. Bernacea, Uganda Department of Veterinary Services, Entebbe.

Release of Sterile Males Alone for Eliminating Low-Level Populations

In estimating the potential possibilities of sterile-male releases for tsetse fly control or eradication, no attempt has been made to consider the many variations in life history, behavior, preferred ecological environments, or other aspects that would, of course, have to be taken into account in developing procedures for specific kinds of tsetse flies. Instead, a hypothetical species and hypothetical conditions have been established, which are assumed to be reasonably representative of the various species. The assumption for the present is that mass-rearing methods for the insect can be developed. It is also assumed that it will be possible to induce complete and irreversible sterility in the males without serious adverse effects on the ability of the released males to compete with normal wild males in mating with the normal wild females. A period of 3 months is regarded as the time required for one complete generation, including the average length of life of the flies. The maximum net increase potential of a tsetse fly population is assumed to be 50 percent per generation. In efforts to make an appraisal of the conditions where the sterile-male-release method might prove to be feasible and practical, tsetse fly populations are classified into four categories, as follows:

(1) High-density population, averaging about 1,000 flies per square mile for the area as a whole; (2) moderate-density population, averaging about 500 flies per square mile; (3) low-density population, averaging about 200 flies per square mile; and (4) minimum-survival population levels, averaging 10 flies or less per square mile.

In extremely low population situations, the mere detection of the presence of an infestation may be difficult and costly, because of limitations in detection methods. In this regard, detection of the presence of insects at low-density levels is often one of the most difficult problems to deal with in the final stages of eradication efforts for most insect species.

From the standpoint of control or eradication, it is assumed that for selective residual spraying, airplane application of mist sprays, or brush clearing, the cost per unit area to achieve eradication will likely be essentially the same whether the tsetse fly populations are high, moderate, or low.

From the standpoint of eradication by the release of sterile males, however, the assumption is made that the cost of eradication will be in inverse proportion to the natural population density. This is the chief advantage of the sterile-male method that needs to be fully exploited in connection with the eradication or control of tsetse flies, as well as other insects. It represents a feature that may permit practical use of the sterile male method alone, as the primary and most practical means of control or eradication in some situations, but perhaps more often prior reduction of high or moderate populations by the use of insecticides or other methods would be necessary or advantageous. The use of sterile males may then become more economical than continued use of insecticides until eradication is achieved.

In order to estimate the possible effect of sterile-male releases alone on tsetse fly population trends, a mathematical model has been established on the basis of the various assumptions made in the foregoing discussion. A low-level population averaging 200 flies per square mile has been chosen as the natural population density for the model. The calculations are shown in model 11. If the natural male population is outnumbered 3:1 during the first 3-month period (or generation), a downward trend in the population would theoretically result, permitting a reduction in the number released each subsequent period until elimination is achieved by the end of a year. It is the assumption in this model that the releases are reduced by one-half each period. Since the theoretical rate of decline in the natural population is greater than the reduction in sterile males released, the ratio of sterile to fertile males will gradually increase.

On the basis of the population dynamics of tsetse flies in general, we could expect an initial release rate as low as 1:1 to start a downward trend in the natural population. However, the 3:1 ratio was selected so that the estimates would be as conservative as possible. A point that should be mentioned is that older females, already mated before sterile males are released, would not be affected if monogamous mating by females is the rule. Therefore, male releases could only begin exerting effects on the overall reproductive potential of the population as virgin females emerge from pupae. Thus, the full impact of the releases will not begin to be felt until older, previously mated females decline because of normal environmental resistance factors. In actual practice, therefore, the effect on population trends will be delayed in the beginning. Theoretically, however, the effects of the releases should extend beyond the period indicated by virtue of some survival of released males beyond the time indicated. From a practical standpoint, these should be compensating factors so far as the number of insects and time required to achieve elimination of a population are concerned. The figures in model 11 indicate that the release of about 1,700 male tsetse flies during the course of a year should eliminate a low natural population. This in itself is encouraging, since there are no doubt many situations where such low levels on the average would occur in large infested areas. However, there would appear to be a number of advantages to the use of at least one insecticide mist spray prior to the use of sterile insects. Therefore, integrated programs of sterile insects and insecticides will be considered next.

The Use of Sterile Males Integrated with Other Control Methods

Under conditions where the average population density of tsetse flies is high (1,000 or more per square mile), the sterile-male-release method should prove useful as an adjunct to chemical control procedures, or chemical control might be regarded as the adjunct to the sterility method. The research by K. S. Hocking and associates of the Tropical Pesticide Research Institute, Arusha, Tanganyika, has shown that two or three airplane sprays will drastically reduce natural population densities, even though 6 to 8 treatments may be required for eradication. Under circumstances where the natural population of tsetse flies in an area is too high to manage economically with sterile-male releases alone, the prior application of several airplane mist sprays

Model 11. —Theoretical trend of a low-density tsetse fly population, averaging 200 flies per square mile, when subjected to sterile-male releases at the rates and periods indicated

Period	Natural population density at beginning of each period	Number of sterile males released each period	Estimated average ratio of sterile to fertile males	Assumed natural population density at the end of each period 1/
0-3 months	200 (100 males + 100 females)	900 (300 per month)	3:1	75
4-6 months	75 (37 males + 37 females)	450 (150 per month)	4:1	22
7-9 months	22 (11 males + 11 females)	225 (75 per month)	7:1	4
10-12 months	4 (2 males + 2 females)	112 (37 per month)	16.5:1	1

1/ In calculating the theoretical effect of the sterile-male releases, it is assumed, as explained in the text, that the released males are fully competitive with normal wild males and exert full effect in reducing the reproductive potential of the total population. The assumption is also made that in the absence of control efforts the natural population from a low level would increase by 50 percent each 3-month period (each generation). Thus, in the absence of sterile-male releases, the population trend would be as follows: First period, 200 flies per square mile; 2nd period, 300 flies per square mile; 3rd period, 450 flies per square mile; 4th period, 675 flies per square mile.

should reduce the natural population to levels that could then be readily managed with relatively few sterile males. We will assume a natural adult population of 1,000 and a like number of pupae of all ages in the soil that will complete emergence within 30 days, and a prelarvipositional period of 15 days for newly emerged females. A series of adult spray treatments at 15-day intervals should virtually eliminate all adults present before treatment, and the adults that emerge from pupae present in the soil, prior to treatment. Such insecticide treatments in all probability would destroy 99 percent of the adults, and reduce reproduction to this extent. If we assume a daily emergence rate of 30 flies per day (15 males and 15 females) before treatment began, we can assume that the daily emergence rate during the 31st to 60th day would be reduced to an average of not more than 0.3 flies per day.

The liberation of a few hundred sterile males per square mile during a period of about 6 months after the last insecticide treatments, should eliminate the remaining population, and achieve the same result as three to five additional insecticide mist treatments.

If, through research, a rearing and release cost factor of 5 cents per male fly could be realized, and if 300 sterile males per square mile would be adequate to complete eradication of the remaining population, an investment of $15 for sterile males would be equal to an investment of from $300-$500 in additional insecticide treatments.

The potential value of sterile male tsetse flies in an integrated program of the type proposed is clearly indicated. However, by taking full advantage of the effect of properly timed, sterile-male releases, in relation to the biology of tsetse flies, it would seem likely that moderate-to-high populations of tsetse flies could be readily eliminated by employing only one insecticide mist treatment, followed by the release of sterile males.

We might assume a natural population density of 500 tsetse flies per square mile, and an emergence rate of 16 flies per day from pupae already in the environment. A single mist spray should destroy 99 percent of the reproducing adults. Thus, sterile males released would have to compete only with the fertile males emerging from pupae and the few survivors of the insecticide treatment.

At an emergence rate of 8 males and 8 females per day, the release of 300 sterile males per square mile would provide an estimated ratio of about 30 sterile to 1 fertile male on the first day after the insecticide treatment. These males would be competing for matings with 8 newly emerged virgin females. By the 30th day, when pupal emergence from the pretreatment population has been completed, the number of fertile males that have accumulated would approach the number of sterile males. However, allowing for some natural mortality, it is likely that the ratio of sterile to fertile males would still be as high as 300 to 200. Thus, on the 30th day, about 3 of the 8 newly emerged, virgin females would be expected to mate with fertile males. It is estimated that the maintenance of a sterile male population at a level of about 300 per square mile would, during the first 30 days, lower the reproductive potential of the natural population by about 90 percent.

Thus, the daily emergence rate from the 46th to 90th day would probably not exceed 2 flies per day (one male and one female). In view of the assumed 15-day prelarviposition period, relatively few flies would emerge during the 31st to 45th day.

A rough estimate indicates that the continued maintenance of a sterile-male population at a level of 300 per square mile, would further reduce the reproductive potential of the population during the 46th to 90th day by about 80 percent. Even though the emergence rate of new flies would be low during this period, a considerable number of the males accumulating during the first 30 days would be expected to survive. In order to assure a further substantial lowering of the reproductive potential of the population, it would be necessary to maintain a fairly high sterile male population during the period mentioned.

If the reproductive potential of the population emerging during the 46th to 90th day is reduced by 80 percent, the emergence rate per square mile on the average should not exceed one fly each 2 to 3 days during the 6-week period following the 90th day. By that time, most of the relatively few fertile females that did mate and most of the males emerging during the first 30 days would have disappeared owing to age. Therefore, it is estimated that the maintenance of a sterile male population at a level of about 100 per square mile for 3 additional months, and at a level of 50 per square mile for the subsequent 3 months, should eliminate the hypothetical population.

The establishment of a model to calculate the effects more precisely would be rather difficult. The writer will not attempt to develop such a model. However, the estimated effect of such an integrated program on a tsetse fly population is probably sufficiently accurate to conclude that about 1,000 to 1,500 fully competitive sterile males per square mile would be adequate to eliminate a moderate population of tsetse flies following one insecticide mist treatment. However, if we assumed that 1,500 would be required, and if the cost per male insect released were 5 cents each, the total cost for the sterile insects would be only $75. If the single mist treatment costs $100, the total cost for elimination would be $175 per square mile. This would represent a highly favorable cost figure in comparison with the estimated $500-$800 that would be required if insecticides alone were employed.

Mass-Rearing of Tsetse Flies

If the foregoing is a realistic appraisal of the number of sterile males that would be required to eliminate tsetse fly populations under different circumstances, it then becomes a matter of major importance to develop methods of rearing tsetse flies at reasonable cost. There should, however, be other advantages besides cost. A program of eradication based primarily on the use of sterile insects would avoid or minimize the adverse effects on other natural fauna that can result from the use of insecticides, brush clearing, and game destruction methods.

On the basis of available information, it is assumed that an average cost of $500 per square mile is necessary to achieve tsetse fly eradication by the application of selective residual insecticides to the vegetation in the tsetse fly environment. The elimination of populations by applying airplane mist sprays would probably average a like amount, or more. Actual cost will no doubt vary greatly, depending on a number of factors, and further research and experience may lead to reductions in cost of eradication by the use of insecticides.

As previously stated, the difficulties and assumed high cost of rearing tsetse flies are regarded as the major obstacles to the practical utilization of the sterile-male-release method for tsetse fly control. The reproductive potential of tsetse flies is extremely low. There is no doubt that this inherent limitation is an important factor. However, the writer is of the opinion that the importance of this factor has been over-emphasized, and that there is reason to believe that, through a concerted research effort with a view to the development of economical mass-production methods, it will be possible to rear the insects at a cost that would fall well within the range of practicability. Based on information supplied the writer by J. Ford of the Department of Veterinary Services, Salisbury, Southern Rhodesia, it may even be feasible to collect pupae from high-density areas at a cost that would be practical for limited use of sterile flies. Collecting male flies from high-density areas for subsequent sterilization and release in areas to be reclaimed may also be feasible.

If a rearing cost of 5 cents per male could be attained, and if, as indicated in model 11, only about 1,700 sterile males would be required to eliminate populations averaging 200 flies or less per square mile in the total area requiring treatment, the cost for the flies would amount to only $85 per square mile. This cost plus all other costs, including the distribution of the insects, probably would not exceed $125 per square mile—a highly favorable figure in relation to costs for chemical control. If this estimate is realistic, the sterility method alone would be more economical than chemical control procedures when natural population-density levels exceed 200 tsetse flies per square mile. However, there would appear to be some advantages to the use of at least one insecticide mist treatment when the natural population is moderate-to-high. The release of large numbers of sterile males might, temporarily at least, add to the hazard of the insect. By prior destruction of the existing adult population, the subsequent addition of sterile males in numbers proposed, would not equal the original total population.

Even though the low reproductive potential of the tsetse flies will limit the number that can be mass-reared, there are certain compensating factors that, in the final analysis, may place tsetse flies in a category comparable to that of certain other insects as favorable candidates for the practical application of the sterile-male technique.

In considering the release of sterile males for insect species having a high reproductive potential, the writer estimates that the initial natural population of males must be exceeded by at least 10 sterile males in order to achieve a downward trend in

the natural population. For tsetse flies, because of their low reproductive potential under natural conditions, as well as under laboratory conditions, an initial matching population of sterile males may be adequate to start a downward trend in the population.

In model 11, the initial ratio was established at 3:1 to provide a safety factor that in all probability would be necessary. Several students of tsetse fly population dynamics have pointed out, however, that these insects are generally highly stable in terms of population densities so that there is relatively little fluctuation in average abundance from year to year. For an insect having such a low net increase potential, irrespective of population density, a matching population of sterile males may be equally as drastic in affecting reproduction as a 10 to 1 ratio would be for such insects as the screw-worm fly, fruit flies, and other species. If this should prove to be a valid assumption, then we have, in relation to other insects, a factor of 10 in favor of the method for tsetse flies, which would offset to a great extent the inherently low reproductive capacity of these insects.

Another factor that could be of major significance in the mass-production of tsetse flies would be the feasibility of utilizing all of the reared females for reproduction purposes. The cost of manually separating males from females probably would not exceed 0.1 cent per male. A cost factor of this magnitude for each individual insect is not now regarded practical in connection with the sterility program for such insects as the screw-worm and tropical fruit flies. For tsetse flies, however, this cost factor would be minor in relation to the total production cost that may be practical. Moreover, it is possible, if not probable, that the release of males only would result in greater efficiency of the sterile insects than the release of both sexes. It may also be desirable, or even necessary, to release males only in certain situations so as to minimize the extra hazard that large releases of sterile flies may create.

Thus, in a mass tsetse fly rearing program, it is proposed that all of the females produced be used for reproduction, and most of the males harvested be used for releases. Since the males of most insects have the capacity to inseminate many females, it seems probable that a low male-to-female ratio in the brood colony would be satisfactory. If each female only averaged slightly more than two progeny during its life, the number of males required for release, and the number of females required to maintain adequate production, automatically would become properly balanced, provided a low ratio of males would insure fertilization of the females. Therefore, the objective in research should be to develop the most economical way to maintain an adult colony on essentially a self-sustaining basis, with just enough surplus males to insure adequate fertilization of the females. The writer has communicated with Mr. J. Ford of the Department of Veterinary Services, Salisbury, Southern Rhodesia, to obtain his views regarding the feasibility of rearing tsetse flies in large outdoor cages or in a natural high-population environment suitably modified for maximum fly production. Research along these lines is underway.

Production costs for tsetse flies at a level of about 5 cents per male, or $50,000 per million, should make the use of sterile tsetse flies well within the range of practicability under a wide range of circumstances.

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